Origin, phylogeny and evolution of pineapple species.

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ORIGIN, PHYLOGENY AND EVOLUTION OF PINEAPPLE SPECIES.
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ABSTRACT - A brief bibliographical update on the classification and origin of pineapple species is followed by discussion of IRFA results on analysis of the genetic resources of the genus in order to propose continuous evolution of the plant, accounted for by the use of sexual reproduction of natural populations organised in complexes of species. This results in a dynamic viewpoint which stands out from the numerous static classifications found hitherto in the literature.

ORIGINE, PHYLOGENIE, EVOLUTION DES ESPECES DU GENRE ANANAS.
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RESUME - Après un bref rappel de l'état des connaissances bibliographiques sur la classification et l'origine des espèces d'ananas, l'auteur se base sur les résultats obtenus par l'IRFA en matière d'analyse des ressources génétiques du genre pour proposer une évolution continue de la plante expliquée par l'utilisation de la reproduction sexuée au niveau des populations naturelles organisées en complexes d'espèces. Il en ressort une thèse dynamique qui se démarque des nombreux essais de classifications à caractère statique trouvés jusqu'à présent dans la littérature.

KEY WORDS : *Ananas*, taxonomy, phylogeny, evolution, species, *Ananas comosus*, natural distribution.

The genus *Ananas* is part the Monocotyledoneae group, the Farinosea order and the Bromeliaceae family. Many attempts at classifying the various forms - edible or not - have appeared in the literature since the 18th century. The various authors mention anything from a single species (with numerous sub-species or varieties) to nearly ten. The classification criteria used concern the various phenotypes of leaf spines, the appearance of the fruit and details of certain parts of the inflorescence.

A good chronological review of all these taxonomic studies was proposed by Antoni in 1983, who thus introduced the classification used today. This classification was the work of Smith, who in 1979 revised his 1939 key using the observations made by Camargo on two new types : *A. fritzmuelleri* (1943) and *A. parguazensis* (1968). Today's classification (table 1) thus comprises 8 species :

- *Ananas comosus*, the cultivated species with large fruits and a short, thick spike.

- *Ananas monstrosus* differs from *comosus* in that there is no leaf formation on the fruit.

- *Ananas bracteatus* has well-developed, bright red flower bracts. The fruit is edible and relatively large.

- *Ananas fritzmuelleri* with pale green, developed bracts. The petals bear special appendices found only in the neighbouring genus *Pseudananas* and some varieties of *A. comosus* (Mordilona group).

- *Ananas ananassoides*, with small fruits, erect leaves and a long, fairly thin spike.

- *Ananas nanus*, a dwarf species whose phenotype is fairly similar to *A. ananassoides.*

TABLE 1 - The 8 species defined in the genus ***Ananas*** (after Smith, 1979).

A. COMOSUS	- cultivated	Cayenne Queen Pernambuco Spanish Mordilona
A. MONSTROSUS	- crownless	
A. BRACTEATUS	- horticulture	
A. FRITZMUELLERI		
A. LUCIDUS	- fibres	
A. ANANASSOIDES	- «wild»	
A. PARGUAZENSIS		
A. NANUS		

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- *Ananas parguazensis* is also similar to *A. ananassoides*, but different features are its curved leaves, the slope of the spike and the direction of implantation of the leaf spines.

- *Ananas lucidus*, similar again to *A. ananassoides*, has smooth (spineless) leaves from which good quality fibre can be obtained.

The genus *Pseudananas* is frequently associated with *Ananas*. Smith (1979) listed only one species, *P. sagenarius*. It is characterised by vegetative propagation by stolons, the absence of shoots on the stem, limited leaf (crown) development or none at all on the fruit, and practically no increase in volume of the latter after flowering. It dries out at maturity, the individual fruits separate even though they grow from flowers which are bonded at flowering.

The validity of this classification, based mainly on characters (fruit size, leaf spines) whose expression may be affected by ecological conditions can nevertheless be questioned. Most of the species defined are inter-compatible (Collins, 1960 ; Cardin, in press ; Evain, 1988, personal experiments) and the resulting inter-species hybrids are fertile (Collins, 1960). Finally, as can be seen, types whose phenotype differences reside in a small number of characters are classified as distinct species (*A. monstrosus* is similar to *A. comosus* ; *A. fritzmuelleri* is similar to *A. bracteatus* ; *A. nanus*, *A. parguazensis* and *A. lucidus* are close to *A. ananassoides*).

These observations led to some of our work on analyses of the diversity of the genus. This resulted in better identification of the species, the concept of which should be revised, and to an approach to their phylogeny.

AREAS OF DISTRIBUTION OF THE SPECIES

Bibliographical data.

All the literature (Smith, 1979 ; Collins, 1960 ; Bertoni, 1919 ; Leal and Antoni, 1980 c) reports two main regions in which *Ananas* and *Pseudananas* species grow spontaneously (figure 1) :

- one covers the south-east extremity of Brazil, Paraguay and northern Argentina, with specific locations of the genus *Pseudananas*, the species *A. bracteatus* and the species *A. fritzmuelleri*, which is not very widespread. In addition to these species characteristic of the zone, *A. ananassoides* appears to be fairly frequent whereas *A. nanus* is reported to have been identified at a single site ;

- the other region is less clear-cut, broadly covering the left bank of the Amazon basin and including northern Peru, eastern Columbia, southern Venezuela, the Guianas, Surinam and, of course, northern Brazil. This is the specific habitat of *A. parguazensis* and perhaps *A. lucidus*. However, *A. ananassoides* is well represented and *A. nanus* has been observed in French Guiana and Surinam.

The heterogeneity of the sites (relief, rivers, vegetation) in these geographical areas makes possible the cohabitation of species whose characteristic habitats would nevertheless appear to be different :

FIGURE 1 - The centre of origin of the pineapple.

- *P. sagenarius* grows in underwood, in particular near watercourses if they flood only rarely. It prefers shady, rich, moist sites.

- *A. bracteatus* grows at the edges of forests where the shade is not as thick ; however, it can stand total absence of shade if the soil is moist.

- *A. ananassoides*, is the hardiest species ; it will grow in the poor, dry «serrado» soils in Brazil and can withstand very sunny positions.

- *A. parguazensis* grows in fairly moist, slightly shady habitats.

- *A. lucidus* probably grows in underwood, but has rarely been observed under spontaneous conditions. It is known in smallholdings where it is grown for its leaf fibres.

- *A. nanus* has rarely been observed under natural conditions.

- It is difficult to define the preferential environment of *A. comosus* as man has introduced it to sites with very varied characteristics.

In situ observations.

Field observations were made during a series of prospection operations carried out in Venezuela in 1985 in natural diversity zones for pineapple (Leal *et al.*, 1986 ; Pinon, 1986 ; Loison-Cabot, 1990).

The plant's facility for survival and development in the absence of man means that it was not possible in all cases to

determine the origin of the populations found. They may be spontaneous or sub-spontaneous forms or escapes.

Thus, although the great diversity of pineapple types cultivated for the fruits (*A. comosus*) or for the leaf fibre (*A. lucidus*) can be assessed from an inventory of the plants in smallholdings near villages, other forms - of less interest as crops - should be sought in their natural propagation areas in the Amazon forest.

In this context, phenotypes similar to *A. ananassoides* were collected in the upper Orinoco basin (VE 15, VE 138, VE 141) in the heart of the Venezuelan part of the Amazon region. A wild type (VE 10) whose habit and fruit are similar to those of *A. ananassoides*, but whose leaves display «piping», was also observed. Enzymatic analysis of this clone shows that the genotype is similar to Péroléra individuals. It might be a spontaneous form from which this variety was derived. *A. ananassoides* thus appears to be fairly polymorphic, and Smith's key cannot be used to classify all the types collected.

A. parguazensis, found in the «Llanos» region on the right bank of the middle course of the Orinoco (VE 8, VE 131, VE 135) cohabits with *A. ananassoides* (VE 23). Neither species could be characterized by sampling of the genes studied using electrophoresis. One of the main differences between them is the orientation of the spines on the leaf. Both display broad enzymatic polymorphism.

A. bracteatus was not found in the areas prospected, and neither were *A. fritzmuelleri* and *A. nanus*, neither of which is very widespread.

With reserves as to the truly spontaneous origin of all the species listed, it can therefore be observed that the following species cohabit in the geographical area visited in Venezuela :

- *A. ananassoides* and *A. parguazensis* in all the drier zones (right bank of the Orinoco, Bolivar State).

- *A. ananassoides* and possibly *A. lucidus*, whose cultivation by the Yanomani indians suggests a close differentiation zone, in the much wetter Amazonas state.

Various forms of *A. comosus* are cultivated in both areas.

NATURAL SEXUAL REPRODUCTION OF PINEAPPLE

Pineapple is known to be a plant with marked preferential vegetative reproduction under natural conditions. This feature has made a considerable contribution to its spread throughout the world and forms the basis of the cultural systems designed for cultivating species of the genus.

However, a number of features, biological data and experimental results tend to show that sexual multiplication of pineapple is also possible under natural conditions.

Biological data.

Numerous pineapple breeding programmes based on hybridization techniques (Collins, 1960 ; Chan, 1986 ; PY *et al.*, 1988 ; Cabot, 1986, 1987, 1988) have made it possible to verify experimentally that the pineapple produces functional gametes. However, according to Cardin (1990), most of the species (except for *A. bracteatus*) and varieties are probably self-incompatible. Previously, only *A. comosus* had been reputed to be self-incompatible (Collins, 1960 ; Pickersgill, 1974). As a system of gametophytic incompatibility (Bhowmik, 1975, 1982 ; Kerns *et al.*, 1932 ; Majumber *et al.*, 1964 ; Gorrez, 1966 ; Brewbaker and Gorrez, 1967 ; Evain, 1988 ; Cardin, 1989) intervenes in most of the cultivated varieties used as clones, self-fertilization does not function and the parthenocarpic fruits are sterile.

In fact, spontaneous inter-crosses are possible on condition that different types co-exist. Fruits with seeds were observed during prospection operations in the Venezuelan Amazon area and in the IRFA collections in Côte d'Ivoire and Martinique where free fertilization can occur between several juxtaposed genotypes.

There has been little study to date of the factors affecting the conservation and germination of the seeds formed during these compatible crosses. They nevertheless govern the effectiveness of sexual reproduction.

Hybridization programmes showed that there is apparently no dormancy in pineapple seeds (Loison-Cabot, 1988). These results were confirmed by germination tests of batches of seeds produced by free fertilization of the inflorescences of various species kept in collections in Côte d'Ivoire (personal work) and Martinique (Cardin, personal communication). The seeds are not viable for very long. Longevity has been estimated to be less than 6 months under the conditions of storage of hybrid seeds obtained in Côte d'Ivoire (Loison-Cabot, 1990).

Characterization of the seed, related to optimal storage conditions, is an important factor involved in the effectiveness of the mechanisms which come into play in sexual reproduction. In fact, it is not known whether the seeds are orthodox or recalcitrant. The absence of dormancy, longevity of less than 6 months in the storage conditions used, the relatively long sexual cycle (approximately 3 years to reach fruit production) and the tropical distribution of the plant might argue in favour of recalcitrant seed, as is seen in many other tropical fruits (mangosteen, mango, rambutan, cocoa, coffee, coconut, etc.) (Chin, 1978).

Apparently reduced longevity of the seeds, relatively long, delicate germination, vulnerable seedlings and a long sexual cycle all appear to be factors which limit reproduction by seeds. The genus appears to compensate for this handicap by active vegetative reproduction.

Nevertheless, crosses between different varieties are sometimes very fertile (several hundred seeds per inflorescence). The number of seeds which can statistically enable the development of a new genotype by natural germination and growth of the plantlet into an adult plant is not zero but is very small. Paradoxically, the plants obtained sexually probably display a high probability of survival and

the conquest of new ecotypes by means of the very effective asexual multiplication which follows.

Experimental results.

Several experimental approaches have provided information on the hypotheses put forward concerning the potential of sexual reproduction of pineapple.

The observation of types *in situ* in a natural propagation zone of pineapple gave the first data. The different zones prospected in Venezuela from Amazonia (SW) to Gran Sabana (SE) along the right bank of the Orinoco revealed a great diversity of types collected, consisting of a mixture of natural populations of *A. ananassoides* and *A. parguazensis*, cultivated varieties of the species *A. comosus* and *A. lucidus* and intermediate types (Loison-Cabot, 1990).

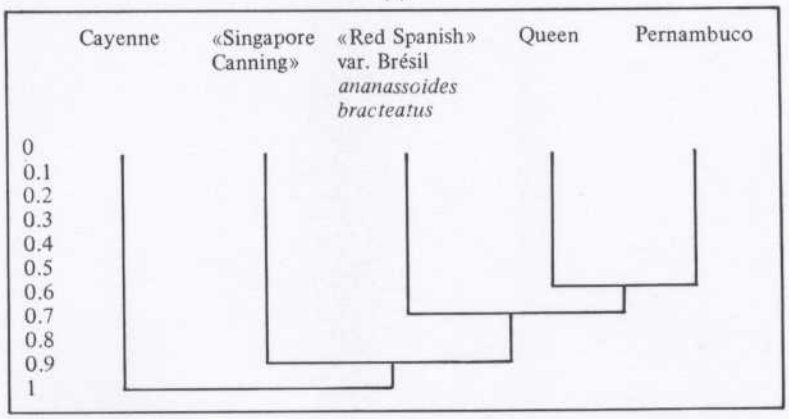
More detailed studies using all the clones in the collections maintained by IRFA and enriched with the new types found in Venezuela were then performed in the laboratory and subjected to factorial analysis of the data. Characterization of the clones using phenotypic observations of production, appearance and quality of the fruits was undertaken first (Loison-Cabot, 1988). The distances between the cultivars evaluated using agronomic criteria (Table 2 a) revealed the existence of a special classification group containing the types found in Brazilian ecosystems in a natural state (Brazilian variety in the dendrogram). This group probably forms a connection between cultivated forms ('Red Spanish' variety of *A. comosus*) and spontaneous forms (*A. ananassoides, A. bracteatus*).

An identification study of the clones using biochemical markers was carried out in parallel by Garcia (1988). Eight enzymatic systems were retained ; in addition to considerable polymorphism, these revealed the proximity of certain genotypic structures characterizing cultivated varieties with large fruits and wild forms with small fruits (Table 2 b).

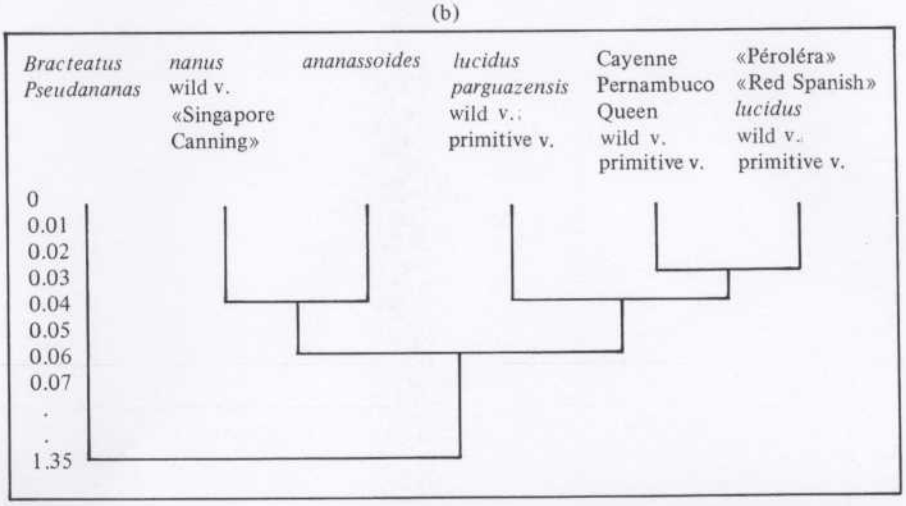
TABLE 2 - Hierarchical cluster analysis calculated from the coordinates of correspondence factorial analysis (diagonalised chi-squared distance matrix) :
(a) using phenotypic characters
(b) from enzymatic systems

Legend : *lucidus*, species ; Cayenne, cultivar ; «Red Spanish», variety.

(a)



(b)



Far from being contradictory, the results obtained by direct evaluation in collections and by biochemical evaluation were complementary and showed the existence of gene exchange between the wild and cultivated forms. This led to observing a particular group of primitive Brazilian varieties revealed by phenotypic observations.

Pineapple is thus not only biologically able to use natural sexual multiplication, but also uses this potential in order to evolve.

An identical ploidy level (2N), compatible reproduction mechanisms and similar habitats lead to considering that there are no reproductive barriers between the wild and cultivated types. The variability observed in Venezuela shows the reality of such gene exchanges.

ORGANIZATION AS COMPLEXES OF SPECIES AND EVOLUTION OF THE GENUS

The basis of organization.

Having demonstrated the specificity of the cohabitation of certain species and the probable existence of gene flows between them, the organization of the genus *Ananas* can be seen as the co-existence of several complexes of species and their compartments envisaged on the basis of the definitions proposed by Pernes (1984) :

«Two plants belong to the same complex if they can, under natural conditions, with non-null probability, exchange genes by hybridization, directly or through intermediate plants».

«Two plants of the same complex belong to different compartments if there are limits to the success of their spontaneous hybridization».

Such a species complex of the genus *Ananas* could be located in the areas prospected in Venezuela. We identified two compartments of this complex characterized by two different habitats. One is in the Amazon zone (*A. ananassoides, A. lucidus* and *A. comosus*) and the other is in the savanna (*A. ananassoides* and *A. parguazensis*). They are geographically close.

The species *A. bracteatus* appears to be genetically very different (according to the enzyme systems studied) from all the populations described above. The distribution area, located in south-west Brazil in the Mato Grosso and along the banks of the Rio Parana, covers habitats which are intermediate between those of *A. ananassoides* (fairly dry, poor zones) and *Pseudananas sagenarius* (wet zones). These two species, together with *A. nanus*, observed in the same geographical zone of the Mato Grosso east of the Rio Paraguay (Collins, 1960), may form with *A. bracteatus* a second complex of species of the genus *Ananas* (figure 2).

However, there may be other complexes of species or, more probably, other compartments with eastern Columbia and northern Peru connected to the Amazon complex.

Within these two complexes, where only geographical remoteness might form an obstacle to the exchange of genes, evolution probably continues independently, permitting among other things markedly contrasted differentiation of *comosus* and other types in the different geographical areas.

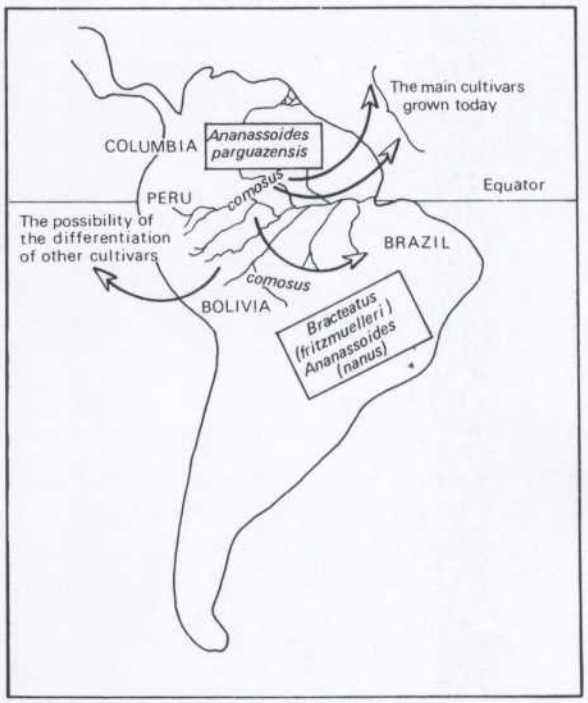


FIGURE 2 - Location of the complex of species of the genus *Ananas*.

Origin of the *comosus* species.

The following basic question is raised . What is the origin of the types with large, edible fruits characteristic of the species *A. comosus* ? Is the answer that of Pickersgill (1974), who said that «the ancestor of *comosus* is *comosus*», meaning that it would theoretically be possible to find this ancestor growing spontaneously, which has not occurred to date. Or is this cultivated species the result of slow evolution oriented towards domestication from partially improved forms resulting from gene exchanges between wild species which still exist ?

The latter possibility is in closer agreement with the hypotheses put forward by other authors. Baker and Collins (1939) observed two particularly vigorous forms of *A. comosus* which appeared to be growing spontaneously in SE Brazil, and suggested that they might form the link between wild and cultivated *A. comosus*. Certain morphological analogies between the types recorded led Bertoni (1919) to identify two lines of evolution in the main species listed :

- *A. bracteatus*, some forms of which are cultivated, may represent a more advanced evolutionary stage than *P. sagenarius*, which the author considered to be an ancestral form. Adaptation to a less shaded, drier environment and the production of a more developed fruit would be the results of this evolution.

- Independently, *A. comosus* and *A. ananassoides* may be a separate branch in which the latter species is the ancestral form. Evolution towards the development of vegetative organs and the acquisition of a number of characters related to domestication were then observed, the latter including the dimensions and quality of the fruit, the shortening and thickening of the spike and the reduction or disappearance of the spines.

The synthesis of these hypotheses, together with the phylogeny proposed by Garcia (1988), and by our demonstration of an organization of the genus in complexes of species, enable us to confirm the hypotheses of two main evolutionary axes in the genus *Ananas*.

The following lines of evolution can be envisaged from *Pseudananas*, the root of the phylogenic tree :

- evolution towards *bracteatus*, which is genetically close to *Pseudananas*. In this complex located in Paraguay, northern Argentina and southern Brazil other forms which have not yet been identified may form relays in evolution towards other large fruit types.

- evolution towards large fruit types which we consider as *comosus* through intermediate forms close to *ananassoides*. Such cultivated types have so far been observed in smallholdings in western Brazil (in the states Acre, Rondonia and Mato Grosso) and in the Amazon basin. Others may be discovered during broader exploration of the sites potentially favourable for pineapple. This differentiation of the type with large fruits from less evolved forms which occurred far from the area occupied by *Pseudananas* assumes that certain forms of the genus migrated to the sites occupied today by the varieties observed.

According to Bertoni (1919), the Guarani people, who left Paraguay, the site of the origin of the genus, spread the cultivation of pineapple across the whole of the American tropical zone as they moved in proto-historic times. The Guarani might thus have been responsible for the migration of partially improved wild forms which constitute the origins of the complex of species located in the Amazon zone during our studies. The types cultivated today would then have differentiated little by little through the continuous fixation of characters interesting for domestication resulting from gene exchanges between improved and wild forms.

There is thus probably no fixed *A. comosus* species which can be found in a spontaneous state, but populations which evolve continuously through introgression between wild and partially improved types from which the types with large, edible fruits differentiated. Certain factors limiting the effectiveness of sexual reproduction slow the evolution of the pineapple populations to a state of equilibrium and account for the variability observed.

Centre of domestication and centre of origin.

Comparison of the observations made *in situ* during prospection work and genotype make-ups deduced from the study of biochemical markers has shown that some of the most domesticated cultivars such as 'Cayenne', 'Péroléra', 'Spanish', 'Pernambuco' and 'Queen' are represented by structures included in all the polymorphism revealed in the plant material prospected.

Thus :

- A plant whose genotype is identical to all the 'Cayenne' clones (VE 11) was found in the Venezuelan Amazon region. However, its phenotype differs from that of 'Cayenne' clones in certain characters of fruit appearance and shape and the «piping» on the leaves. The fruit is large and edible fruit.

- Numerous plants with genotypes identical to certain clones of the Columbian variety 'Péroléra' were also observed in this region near the villages ('Brecheche' variety : VE 1, VE 6B, VE 24, VE 45). The phenotype is different from typical 'Péroléra' plants since, among other features, the leaf piping character of the variety (the edges of the leaves have whitish piping where the upper epiderm is covered by the lower epiderm) is replaced by different smooth leaves.

- A representative of the 'Red Spanish' variety (VE 21) identical to that commonly cultivated throughout the Caribbean zone was found in a smallholding in the extreme south of Amazonia.

- 'Pernambuco' phenotypes (VE 13, VE 16) were frequently observed, but the genotype is not the same as that of the domesticated varieties.

- Finally, a fruit whose eyes, the golden yellow colour of the ripe fruit and genotype are similar to the 'Queen' cultivar (VE 18) can also be mentioned as being cultivated in this region.

Some of the domestic forms widely grown today may thus have been differentiated in the Amazon region.

One of the centres of domestication of the main cultivars, and which is probably close to a centre of diversification may therefore be located between the Brazilian and Venezuelan Amazon and their boundaries. It may in fact correspond to the area that Leal and Antoni (1980) presumed to be the zone of origin. This does not mean that there might not be one of more domestication centres outside this zone. This could apply to the 'Singapore Canning' variety that our studies showed is clearly different to 'Red Spanish', even though it belongs to the same «Spanish» *Ananas comosus* group. No type related to this variety was observed in the Amazon zone, leading to considering that differentiation was independent of that of the other cultivars known.

In addition, the complex characterized by the *Pseudananas* ancestral form probably corresponded to the centre of origin of the genus *Ananas* as proposed by Bertoni (1919) and then by Collins (1960).

THE CONSEQUENCES FOR CLASSIFICATION

These considerations invite us to reconsider the classification used today. The numerous attempts at classifying pineapple types reported in the literature show the hesi-

tations of the authors in proposing reliable structuring of the variability observed by some *in situ* and by others in the simple examination of herbaria.

The key proposed by Smith (1979) enabled him to provide a more or less satisfactory identification of the types available to him. In contrast, application of the key to the types observed during prospection in Venezuela is difficult.

The aim is not to discuss the criteria of identification, some of which are influenced by environmental factors, but rather to re-examine the procedure which, when a new phenotype is identified, involves a new key enriched with new species (cf. the discovery of *A. fritzmuelleri* in 1943 and then of *A. parguazensis* in 1968 by Camargo). These procedures ignore the obvious existence of sexual reproduction in pineapple, and attempt to draw up a catalogue of forms which are not in fact fixed.

In the light of the results discussed here, we would tend to considerably reduce the number of species. Most of those listed today are probably a number of the numerous potential versions of a small number of species :

- *A. parguazensis* is similar to *A. ananassoides* and may only be a variety of the latter.

- *A. nanus* appears to be a miniature form of *A. ananassoides*.

- The species *A. fritzmuelleri*, not examined here, is phenotypically close to *A. bracteatus* and not very far away geographically and may be a form derived from the latter species.

- The existence of *A. monstrosus* as a taxonomic entity remains to be demonstrated. The genotypic structure of the crownless fruits observed in Venezuela was the same as that of the normal plants growing in the same sites.

CONSEQUENCES FOR THE ORGANIZATION OF PLANT COLLECTION OPERATIONS

The prospection carried out in the northern part of the Amazon basin on the Venezuelan side has confirmed the considerable diversity of the wild and cultivated types in this region. However, this zone, which we suppose to be a domestication centre for the cultivars grown today, extends towards Brazil and then towards Columbia and Peru where very special local varieties are found.

Other compartments of the complexes proposed may exist, and it would be interesting to visit them. The little-known «northern Argentina, southern Brazil, Paraguay» zone could be explored to index all the spontaneous types there to evaluate the variability expressed.

The sampling to be carried out during collection operations should be better adapted to detecting sexual reproduction, whose probability is non-negligible (inspection of seeds in rotten or dry fruits and search for seedlings resulting from sexual reproduction). The interest of sampling any seeds found in the fruits examined *in situ* should also guide the choice of season for future prospection in the light of the production period which is induced naturally by the climatic conditions (length of day, temperature).

REFERENCES

ANTONI (M.J.). 1983.
Taxonomy and cytogenetics of pineapple.
Ph. D. Thesis, Univ. Florida, 78 p.

ANTONI (M.G.) y LEAL (F.). 1980.
Clave para la identificación de las variedades commerciales de piña (*Ananas comosus*).
Rev. Fac. Agron. (Maracay), Alcance 29, 13-24.

BAKER (K.F.) and COLLINS (J.L.). 1939.
Notes on the distribution and ecology of *Ananas* and *Pseudananas* in South America.
Amer. J. Bot., 26, 697-702.

BERTONI (M.S.). 1919.
Contribution à l'étude botanique des plantes cultivées. I.- Essai d'une monographie du genre *Ananas*.
Anales Científicos Paraguayos, serie II (4), 250-322.

BHOWMIK (G.). 1982.
Self incompatibility in pineapple.
Ind. J. Genet., 42, 345-347.

BHOWMIK (G.) and BHAGABATI (A.). 1975.
Self-incompatibility studies in pineapple (*Ananas comosus* L.).
Ind. Agric., 19, 2, 259-265.

BREWBAKER (J.L.) and GORREZ (D.D.). 1967.
Genetics of self-incompatibility in the monocot genera, *Ananas* (pineapple) and Gasteria.
Amer. J. Bot., 54 (5), 611-616.

CABOT (Chantal). 1987.
Practice of pineapple breeding.
Comm. Symposium on Tropical and Subtropical Fruit Breeding, 29-30 January 1986, Brasilia (Brazil). Acta Horticulturae, 196, 25-36.

CABOT (Chantal). 1987.
Amélioration génétique de l'ananas. I.- Considérations préalables aux recherches conduites en Côte d'Ivoire.
Fruits, 42 (10), 567-577.

CABOT (Chantal). 1989.
Amélioration génétique de l'ananas. II.- Objectif du programme de création variétale entrepris en Côte d'Ivoire et techniques utilisées pour sa réalisation.
Fruits, 44 (4), 183-191.

CABOT (Chantal). 1989.
Amélioration génétique de l'ananas. III.- Sélection de nouvelles variétés par utilisation d'un index phénotypique appliqué à l'analyse d'une descendance hybride issue du croisement entre les géniteurs Cayenne et Péroléra.
Fruits, 4 (12), 655-667.

CAMARGO (F.C.). 1939.
Ananas e abacaxi.
Rev. de Agric., Piracicaba, XIV, 7-8, 3-20.

CAMARGO (F.C.). 1943.
Vida e utilidade das Bromeliaceae.
Inst. Agr. Norte, Bol. Tec. 1 *(Belem)*.

CAMARGO (F.C.) and SMITH (L.B.). 1968.
A new species of *Ananas* from Venezuela.
Phytologia, 16 (6), 464-465.

CARDIN (Marie Luce). 1988.
Communication personnelle.

CHAN (Y.K.). 1986.
Hybridization and selection in F1 as a methodology for improvement of pineapple.
Prosid. Simp. Buah-buaham Keb., Serdang, 307-314.

COLLINS (J.L.). 1949.
History, taxonomy and culture of the pineapple.
Economic Botany, 3 (4), 335-359.

COLLINS (J.L.). 1960.
The pineapple, botany, cultivation and utilization.
Leonard Hill Ltd London, 294 p.

DEMARLY (Y.). 1977.
Génétique et amélioration des plantes.
Ed. Masson Paris, 287 p.

EVAIN (D.). 1988.
Nouvelles données sur l'incompatibilité chez le genre *Ananas*.
DAA ENSA Toulouse, 43 p.

GARCIA (M.L.). 1988.
Etude taxonomique du genre *Ananas*.
Utilisation de la variabilité enzymatique.
Thèse UST Languedoc, 156 p.

GORREZ (D.D.). 1966.
Genetic studies of self-incompatibility in pineapple.
Thesis, University of Hawaii, 50 p.

LEAL (F.J.) and SOULE (J.). 1977.
«Maipure», a new spineless group of pineapple cultivars.
Hortscience, 12 (4), 301-305.

LEAL (F.) y ANTONI (M.G.). 1980 a.
Descripción y clave de las variedades de piña cultivadas en Venezuela.
Rev. Fac. Agron. (Maracay), Alcance 29, 51-79.

LEAL (F.) y ANTONI (M.G.). 1980 b.
Especies del género Ananas : orígen y discribución geográfica.
Rev. Fac. Agron. (Maracay), Alcance 29, 5-12.

LEAL (F.) y ANTONI (M.G.). 1980 c.
Sobre las especies del género Ananas y su distribución especialmente novedosa para Venezuela.
Rev. Fac. Agron. (Maracay), Alcance 29, 43-50.

LEAL (F.), GARCIA (M.L.) y CABOT (Chantal). 1986.
Prospección y recolección de ananas y sus congeneres en Venezuela.
FAO/IBPGR Plant Genetic Resources Newsletter, 66, 16-19.

LINDEN (M.J.). 1879.
Ananas mordilona Linden.
Belgique Horticole, 29, 302-303.

LOISON-CABOT (Chantal). 1988.
Amélioration génétique de l'ananas : exemple de création variétale, analyse des ressources génétiques disponibles.
Thèse, Université Paris-Sud, Centre d'Orsay, 193 p.

LOISON-CABOT (Chantal). 1990.
Prospection sur l'ananas au Vénézuéla.
Fruits, 45 (3), 251-264.

LOISON-CABOT (Chantal). 1990.
Etat des connaissances botaniques, cytogénétiques et biologiques sur la reproduction de l'ananas.
Fruits, 45 (4), 347-355.

LOISON-CABOT (Chantal) and LACOEUILHE (J.J.). 1990.
A genetic hybridization programme for improving pineapple quality.
Acta Horticulturae, 275, 395-400.

MAJUMDER (S.K.), KERNS (K.R.), BREWBAKER (J.L.) and JOHANNESSEN (G.A.). 1964.
Assessing self incompatibility in pineapple by a pollen fluorescence technique.
Proc. of ASHS 84, 217-223.

NETTANCOURT (D. de). 1977.
Incompatibility in Angiosperms.
Ed. Springler Verlag, Berlin.

PERNES (J.). 1984.
Gestion des ressources génétiques des plantes.
Ed. Lavoisier Paris, 2 t., 212 et 346 p.

PICKERSGILL (B.). 1974.
Pineapple, in evolution of crop plants.
Ed. Simmonds Longman, 14-18.

PINON (A.). 1986.
Prospection au Vénézuéla du 20 février au 10 mars.
Doc. int. IRFA, 12 p.

PURSEGLOVE (J.W.). 1972.
Tropical crops.
I.- Monocotyledons.
Ed. Longman, 76-91.

PY (C.). 1949.
Ananas, systématique, origine, dispersion, génétique.
Fruits d'Outre Mer, 4 (11), 407-414.

PY (C.), LACOEUILHE (J.J.) and TEISSON (C.). 1987.
The pineapple, cultivation and uses.
Techniques agricoles et Productions tropicales.
Ed. Maisonneuve et Larose, Paris, 568 p.

SMITH (L.B.). 1939.
Notes on the taxonomy of *Ananas* and *Pseudananas* Bot.
Museum Leaftlets Harvard Univ., 7 (5), 73-81.

SMITH (L.B.). 1979.
Ananas comosus **L. Merr.**
in : *Flora Neotropica*, 14, part. 3, 2048-2064.

VELEZ (I.). 1946.
Wild pineapple in Venezuela.
Science, 104, 2705, 427-428.

VUILLEUMIER (B.S.). 1971.
Pleistocene changes in the fauna and flora of South America.
Sciences, 173, 3999, 771-780.

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Chantal LOISON-CABOT.

Fruits, Jan.-Feb. 1992, vol. 47, n° 1, p. 25-32.

RESUMEN - Después de un breve recordatorio del estado de los conocimientos bibliográficos sobre la clasificación y el origen de las especies de piña, el autor se basa en los resultados obtenidos por el IRFA en materia de análisis de recursos genéticos del género, para proponer una evolución continua de la planta explicada por la utilización de la reproducción sexuada a nivel de las poblaciones naturales organizadas en complejos de especies. Se obtiene una tesis dinámica que se diferencia de los numerosos ensayos de clasificación de caracter estático encontrados hasta el presente en la literatura.